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STUDIES ON RESISTANCE OF PINES TO INSECTS

by

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SUMMARY

Resistance of pines to the pine reproduction weevil and Dendroctonus bark beetles and possibilities of breeding resistant trees have received much study in California. Considerable success has been achieved in empirically identifying species resistant to the weevil, and some progress has been made toward determining the causal mechanism for this resistance. Only promising leads have been obtained in identifying resistance and its causal mechanism for Dendroctonus bark beetles.

Early research indicated that a backcross of P. jeffreyi to a natural P. jeffreyi x P. coulteri hybrid was resistant to the weevil. Substantiated by field tests, this finding has led to the development of a practical breeding program. Variation in resistance within P. ponderosa and P. jeffreyi, two species susceptible to the weevil, is being explored, and the screening of pine species and hybrids continued.

Research on the resistance of pines to Dendroctonus spp. (primarily brevicomis and monticolae) has a longer and more diverse history. Much of the work has been on the role of resin. Forced-attack studies were inconclusive but indicated differences between pine species and hybrids, and suggested that resin could be an important factor. Studies of resin flow showed some relation between duration of flow and the susceptibility of old-growth P. ponderosa and P. jeffreyi to bark beetle damage. Studies of resin quality, as measured by vapor toxicity to adults, suggested that bark beetles can tolerate saturated resin vapors of host but not of nonhost pine species. Resin vapors of hybrids between host and nonhost species were either lethal or toxic enough to reduce feeding. Current studies indicate significant variability in D. brevicomis tolerance to the individual terpenes of its host, P. ponderosa. The terpene composition of the latter varies widely. A small number of phenotypically resistant pines are being vegetatively propagated for study and possibly for breeding. The factor of resin pressure in the success or failure of bark beetle attacks is another subject of research which is being pursued.

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INTRODUCTION

The development of insect-resistant plants has received considerable attention by entomologists and geneticists for more than 60 years, but most of the effort has been on food plants. Only in the past 20 years has anything except cursory attention been given to insect resistance in forest trees. Specific insects investigated include (a) Pissodes strobi (Peck) (Jaynes 1958), (b) Megacoryllene robiniae (Forster) (Hall 1942), (c) Cecidomyia pininopis O.S. (Austin et al. 1945), (d) Rhyacionia buoliana (Schiff.) (Holst and Heimbürger 1955), (e) Chermes cooleyi Gill. (Petersen et al. 1958), and the insects which will be discussed in this paper -- (f) Cylindrocopturus eatoni Buch., and (g) Dendroctonus spp.

Progress has not been particularly rapid because of the comparatively low value of trees, the length of time for a tree to reproduce, and the time necessary for trees to express heritable characteristics. Nevertheless, Beal (1957) concludes that the outlook is promising for breeding resistant trees. He suggests that: (a) breeding for insect resistance should be part of a well-rounded tree breeding program (b) joint effort by entomologists, geneticists, and other scientists will probably give quickest and soundest results, (c) as a means of insect control, resistant trees may do the whole job but more than likely will be part of an integrated system of control, and (d) quickest results will be obtained for pests of tree seedlings; a much longer time will be required for pests of saplings and mature trees.

The development of insect-resistant trees is not without uncertainties. Resistance to one insect does not imply resistance to all; in fact, resistance to one could increase the susceptibility to others. For example, Stevens (1959) reported that Smith found certain pines classed as resistant to Cylindrocopturus eatoni to be among the species most heavily damaged by Zelleria hainbachii Busck. Moreover, insects are variable in capabilities and have short generations; hence, it is possible for them to develop the capacity to overcome the defense mechanisms of plants resistant to their progenitors.

Much of the recent research on resistance of forest trees to insects has centered upon the beetle species discussed in this paper. These species are primary pests of pines, and research on them illustrates some of the progress that has been made, as well as some of the obstacles to developing resistant forests.

THE PINE REPRODUCTION WEEVIL

Research on the resistance of pines to the pine reproduction weevil was started by Miller (1950) in 1946 at the Institute of Forest Genetics in Placerville, California. The weevil is a serious pest of 3 to 10-year-old pines, particularly in plantations. It attacks and kills a large number of pine species, in California most notably Pinus ponderosa Laws. and P. jeffreyi Grev. and Balf., but it is not known to kill P. coulteri D. Don. Miller drew upon this information in his initial studies by subjecting these three species and a backcross of a natural P. jeffreyi-P. coulteri hybrid to P. jeffreyi (P. jeffreyi x (P. jeffreyi x P. coulteri)) to forced attacks of the weevil in 4- to 6-year-old nursery beds. Results of these first tests were gratifying; the weevils attacked all trees, but they were able to kill only P. ponderosa and P. jeffreyi. They were unable to kill either P. coulteri or the backcross hybrid.

Miller also investigated the mechanism of resistance. He found that necrotic tissue develops around the egg puncture in the cortex and that a cork layer develops in the cortex, walling off this necrotic tissue. In trees which were killed, the small larvae penetrated the necrotic tissue and the cork layer and reached the cambium. In trees which survived, the larvae were unable to penetrate the cork tissue. Miller attributed resistance either to this cork layer which develops around the necrotic tissue, or to some property of resin.

Callahan (1960) carried on Miller's studies of testing species and hybrids at the Institute for resistance to weevils. He concluded that there was considerable heritable racial variation in resistance within P. ponderosa. This variation might be used for within-species breeding of resistant trees.

Smith (1960), who continued the work, reports that 11 resistant pine species, varieties, or hybrids had been discovered out of 30 which had been observed in the preceding 15-year period that the host relationship of the weevil had been studied. He found evidence which suggested that the female tree parent is more influential than the male parent in the transmission of resistance to progeny. Research findings to date show that the possibilities for hybridizing pines to produce trees resistant to weevils are considerable. The exact nature of the resistance mechanism and its inheritance, however, are not fully known. The screening of additional species and hybrids is being continued. In addition, studies are in progress to determine the influence of individual parent trees on resistance. Results of such studies could provide the information needed to take some of the guesswork out of the breeding procedures.

Field tests of the backcross hybrid and the two parent species have substantiated findings in the nursery that the hybrid is markedly resistant to weevil attack (Hall 1959). P. jeffreyi was killed by the weevil; P. coulteri succumbed to cold weather.

A large-scale program to produce weevil-resistant stock for planting in northern California was begun by the United States Forest Service 5 years ago (Libby 1958). The breeding program uses P. jeffreyi x P. coulteri F₁ hybrids, and the natural hybrid. Current work is designed to screen a large number of Jeffrey pines for compatibility with Coulter pine genes. Hybrid-producing Jeffrey pines are being grafted into an orchard for subsequent controlled pollinations. Annual production of weevil-resistant hybrids now numbers in tens of thousands, but the goal is several million.

PINE BARK BEETLES

Research on the resistance of pines to bark beetles has followed a longer, more diverse, less successful, and more frustrating course because of certain characteristics of the beetle and pines. Most species of bark beetles seldom attack trees less than 30 years old; the problem of time is obviously great. Moreover, the insect species that are most important develop successfully only in trees that are living when attacked but which die as the brood develops. Since they kill a tree, it is difficult - in fact currently impossible - to measure a partial effect of bark beetle attacks, as is possible with defoliating insects. Also, to test a tree for resistance to bark beetles, one must work with the whole tree, and this entails surmounting sizable physical obstacles.

The species most intensively studied in relation to its host is Dendroctonus brevicornis LeC., which over the years has been the number one killer of P. ponderosa (Miller and Keen 1960). Much of the work has been on the role of resin in the resistance or susceptibility of pines to beetle attack, though other tree characteristics have not been neglected. The visible manifestations of P. ponderosa trees (for example, needle length, complement, color, etc.), which might be indicative of varying degrees of susceptibility, have received a great deal of study. A large body of knowledge on this subject has been synthesized into the ponderosa pine risk-rating system (Salman and Bongberg 1942; Keen and Salman 1942). This system is a means of classifying mature and overmature P. ponderosa and P. jeffreyi trees according to their relative susceptibility to bark beetle attack. Trees so classified were the basis for one of the first intensive studies of the role of resin in resistance.

Resin is considered a secondary plant product, and Fraenkel (1959) feels, with reasonable evidence, that secondary plant products are very important in insect-host selection, susceptibility, and resistance. Certain characteristics of resin (Morgan et al. 1955) have been found to have a high degree of genetic control.

Resin was first theoretically implicated in the resistance of Pinus ponderosa to Dendroctonus monticolae Hopk. by Hopkins (1902). For the next 25 years little was done to explore this possibility. Person (1931), working with P. ponderosa and D. brevicornis, stated that the success of the first attacks on a tree depends on the ability of the beetle to overcome the flow of resin. Gordon^{1/} found that certain constituents of resin were found to be toxic to bark beetles. Thereafter studies of resin in relation to bark beetles lapsed for 20 years.

Resin was implicated as a resistant factor by Miller's^{2/} evaluation of forced attacks by D. brevicornis and D. jeffreyi Hopk. on 20-year-old P. ponderosa and P. jeffreyi and their hybrid. His results were tentative because of the lack of good quantitative values for measuring differences obtained between trees. He concluded that beetles were less successful in attacking nonhost pines than host pines and suggested that the beetles were not able to tolerate nonhost or hybrid resin. Callahan and Miller^{3/} expanded the forced-attack studies to include D. monticolae, and were able to substantiate Miller's earlier findings. They hypothesized that the host specificity of bark beetles was determined by tolerance to resin of host species but intolerance to resin of nonhost species, and that in host species quantity of resin flow became a critical factor in the success or failure of beetle attacks.

Callahan^{4/ 5/} speculated further on the role of both quantitative flow and resin pressure. He undertook an extensive study to relate resin flow to bark beetles' susceptibility as indicated by the risk-rating system. He showed (1955) that flow from a standard wound was prolonged in low-risk trees (those least likely to be killed by bark beetles). He attributed failure of beetle attacks on low-risk trees to a continued flow of resin, but he was unable to associate total flow with susceptibility according to the risk classification. These investigations implicated duration of resin flow and kind of resin produced in resistance of pines to Dendroctonus bark beetles.

Since 1955, basic studies have been in progress to determine whether pine resins are deleterious to bark beetles, what effects they have on tree resistance, and what variations in resins occur within and between species.

Smith (1961a) devised a technique for determining the toxicity of saturated vapors of whole, fresh pine resins to adult bark beetles. Using a limited number of pines and three species of bark beetles, he hypothesized that Dendroctonus beetles could tolerate saturated resin vapors (i.e. the volatile terpenes) of host pines, but not of nonhost pines (Smith 1961b). The hypothesis had to be limited to hard pines because in tests

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- 1/ Gordon, A. Tree injection experiments in white fir and ecological studies of insects attacking yellow pine. U.S. Dept. Agr. Bur. Ent., Forest Insect Lab., Berkeley, Calif. unpub. Prog. rpt. 10 pp., illus.
 - 2/ Miller, J. M. Studies of resistance of pine hybrids to insect attack at Institute of Forest Genetics. U.S. Dept. Agr. Bur. Ent. and Plant Quar., Forest Insect Lab., Berkeley, Calif. unpub. prog. rpt. 15 pp., illus.
 - 3/ Callahan, R. Z. and Miller, J.M. Studies of the resistance of pine hybrids to bark beetle attacks, season of 1951. U.S. Dept. Agr. Bur. Ent. and Plant Quar. Forest Insect Lab., Berkeley, Calif. unpub. prog. rpt., 29 pp., illus.
 - 4/ Callahan, R. Z. Host selection and host susceptibility in the western pine beetle-ponderosa pine complex. U.S. Dept. Agr. Bur. Ent. and Plant Quar., Forest Insect Lab., Berkeley, Calif., unpub. prog. rpt. 8 pp.
 - 5/ Host specificity in the Dendroctonus-Pinus complex. U.S. Dept. Agr., Bur. Ent. and Plant Quar., Forest Insect Lab., Berkeley, Calif. Special report BK-11, 12 pp., illus.

with two soft pines it did not hold true. The resin vapor of the hybrid P. jeffreyi and P. ponderosa (nonhost x host with respect to the beetle) was intermediate between the two parent trees in its effect on D. brevicornis. The hypothesis was substantiated by more extensive testing which included additional pine species and hybrids, and additional beetles (Smith 1961c).

Two hybrids of particular interest were P. jeffreyi x P. ponderosa and P. jeffreyi x P. coulteri. Each is a cross of a nonhost and host with respect to both D. brevicornis and D. monticolae. Resin vapors of these hybrids usually were toxic to D. brevicornis but not to D. monticolae. However, the behaviour of the latter suggested that the vapors had sublethal effects. Consequently, the vapor toxicity procedure was modified so that the beetles were individually confined to tubes of bark within a fumigation jar. The effect of resin vapor on the bark-boring activity of the beetle was assessed by measuring the amount of frass produced. In tests with this technique, the feeding ability of D. monticolae was reduced in the presence of saturated resin vapors of the two hybrids, ^{6/} showing that the vapors do have sublethal effects.

Recent research by Smith indicates considerable difference in the toxicity of the vapors of individual terpenes of resin of host pines to D. brevicornis and D. monticolae. Also, large differences occur in the terpene composition between trees in local populations of P. ponderosa. Vapor toxicity tests, using P. ponderosa differing widely in their terpene composition, indicate that natural combinations of terpenes act like the individual ones; i.e., the greatest toxicity is caused by resin extracts containing the highest proportions of the more toxic terpenes. If this relationship can be substantiated with more extensive testing and possible by field observation, it will provide the geneticist with a valuable tool to circumvent the formidable barrier of time in dealing with bark beetle resistance. Resistant trees may then be located by biochemical screening.

Oleoresin exudation pressure has received some study as an indicator of the susceptibility of pines to bark beetle attack. Vité and Wood (1961), reporting the results of two seasons' work in second-growth P. ponderosa, found that during one season the frequency of tree mortality from D. brevicornis and D. monticolae attacks was six times greater for trees with low oleoresin pressure than for those with high pressure. During the second season, however, the relationship between resin pressure and mortality was not nearly as strong; low-pressure trees were killed less than twice as often as high-pressure trees. The authors conclude that oleoresin exudation pressure is under strong environmental control, but that under certain conditions it is indicative of P. ponderosa susceptibility to bark beetle attack. Whether this is generally true is yet to be proved. The applicability of these findings to other stand conditions and other bark beetle infestations is currently receiving considerable study.

Observations on bark beetle attacks on P. ponderosa in natural stands suggest that some trees may be phenotypically resistant. Scions of trees that have survived heavy bark beetle attack are being propagated vegetatively by grafting. These grafts will be used later for study and possibly for breeding. The trees and grafts will be analyzed for all the resin characters which have been considered as possible factors of resistance.

Past research has been heavily slanted to resin, about which there still is much to be learned. The subjects of attraction, repellency, and nutrition in the bark beetle-pine relationship have been given considerable thought, but comparatively little systematic study heretofore. In the past year, work has been started on the variable capacity of bark beetles to attack pines, which could be equally as important as the variable capacity of the tree to resist beetles.

^{6/} Smith, R. E. Progress report: Resistance of pines to bark beetles, studies on toxicity of resins, 1961. U.S. Forest Serv. Pac. Southwest Forest and Range Expt. Sta., Berkeley, Calif., 20 pp., illus.

Therefore, despite considerable work and progress, we are not to the point where breeding pines for resistance to bark beetles can be conducted with confidence. In fact, it is not yet possible to identify a resistant tree. We are not sure what to look for, but we suspect the kind and amount of resin to be critical. Future prospects for identifying and breeding resistant pines appear somewhat brighter than a few years ago.

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